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Overland movement and migration phenology in relation to breeding of Arctic Terns *Sterna paradisaea*

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Link to published manuscript:
https://onlinelibrary.wiley.com/doi/10.1111/ibi.12723

It is often implicitly assumed that seabirds migrate using marine environments, but this assumption is increasingly being challenged by electronic tracking data. The arrival and departure routes of Arctic Terns breeding on the North Sea coast of the United Kingdom (UK) are unknown but there has been speculation about the possibility of overland migration. Analysis of light-level geolocator data from birds breeding on the Farne Islands suggests that these birds arrived and left their North Sea colony overland via the Irish Sea, rather than taking coastal routes along the east coast of the UK and through the English Channel. In addition, some departing birds may enter the North Atlantic by crossing Ireland rather than through the Irish Sea. The direction of arrival in spring had a more-southerly orientation than the direction of autumn departure. The geolocator data allow migration phenology in relation to breeding to be defined and indicated that the birds arrived around 15 days before the first eggs were laid in the colony. Departure timing may be determined by seasonal progression and not markedly influenced by breeding success. This study supports the idea that overland migration may be a more widespread and consistent strategy for seabirds than has been realised.

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Key Words: Light-level geolocator, Irish Sea, Farne Islands, North Sea

With 70% of the global surface represented by ocean, it is not obvious that seabirds would regularly cross land on migration if over-water routes are available. However, new tracking technologies are beginning to reveal that many seabirds do not conform to expectation. Inexperienced juvenile Streaked Shearwaters *Calonectris leucomelas* migrate south directly across Honshu Island, Japan, apparently using an innate compass orientation, in contrast to adults which skirt around landmass obstacles on southward migration (Yoda *et al.* 2017). Land and mountain ranges may not represent a barrier for the migration of experienced seabirds: geolocator-tagged Arctic Terns *Sterna paradisaea* from an Alaskan colony travelled from the Pacific to the South Atlantic Ocean across the southern Andes of South America (Duffy *et al.* 2013). A regular overland migration route for marine birds from the Gulf of Mexico to the Pacific has recently been identified (Lamb *et al*. 2018) and there is long-standing evidence for the trans-Pennine migration of Common Terns *Sterna hirundo* and Sandwich Terns *Thalasseus sandvicensis* across the United Kingdom (UK) from the North Sea to the Irish Sea in autumn (Ward 2000, Wernham 2002). Furthermore, Long-tailed Skuas *Stercorarius longicaudus* may migrate across the UK in spring (Wynn *et al.* 2014). While taking a direct overland route between different marine resources may be an easy strategy for a seabird, man-made obstacles such as wind farms represent unnatural hazards with potentially unexpected conservation implications which need to be recognised (Lamb *et al*. 2018). Therefore, it is important to identify the routes and extent of overland movements as components of the migration strategies of seabirds.

Arctic Terns have a circumpolar breeding distribution in the northern hemisphere. The UK holds approximately 10% of the world breeding population (Mitchell *et al.* 2004) and the North Sea coast of Northumberland has around 4000 breeding pairs (Redfern 2017). This species has one of the longest migrations known, migrating each year to the Antarctic via coastal waters off the west coast of Africa after breeding in the northern hemisphere (Egevang *et al.* 2010, Fijn *et al.* 2013). In the UK, Arctic Terns are at the southern limit of their breeding distribution but breed on the west and east coasts with colonies on both sides of the Irish Sea (Mitchell *et al.* 2004). As a seabird that feeds on small surface fish and marine invertebrates, it has been assumed that Arctic Terns migrate to the southern hemisphere and back each year via coastal routes (Fisher & Lockley 1954). Therefore, Arctic Terns breeding on the east coast of the UK might travel between the North Sea and the Atlantic via the English Channel. Although there is indeed a regular passage of Arctic and other terns through the English Channel in spring and autumn (Vinicombe 2014), analyses of inland sightings of Arctic Terns have led to speculation that some birds may migrate across the UK, perhaps in response to particular weather conditions (Kramer 1995, Vinicombe 2014). To test the hypothesis that Arctic Terns from a North-Sea colony follow mainly coastal routes to and from their breeding colony, we analysed data from a geolocator study of Arctic Terns breeding on the Farne Islands, Northumberland.

METHODS

Study area and attachment of geolocators

Arctic Terns were trapped on the nest within the courtyard area of Inner Farne (longitude -1.656; latitude 55.617) in 2015 (28 birds) and 2017 (25 birds). Birds were fitted ('tagged') with geolocators (Migrate Technology Ltd, Cambridge, UK; Intigeo-W65A9-SEA) attached to dark-green plastic ('Darvic' PVC) leg rings bearing a white two-digit number using nylon cable ties, self-amalgamating tape and epoxy resin (Table 1). PVC cement (Evo-Stik 'Pipe Weld') was used to seal the ring after fitting. The geolocator and ring assemblies weighed ~ 0.95 - 1 *g*, which represented a mean of 0.92 ± 0.05% sd of the bird body mass when fitted. Geolocators were orientated along the long axis of the leg, and the ring with attached geolocator rotated freely. The study was licensed by the Ringing Scheme of the British Trust for Ornithology (BTO). All except two nests (both in 2015) were monitored during the season by National Trust Rangers on the Farne Islands as part of their regular monitoring work. Regular ringing and retrapping has shown that in subsequent years Arctic Terns within this colony have a high probability of returning to within a few metres of their previous nest (Redfern, unpublished); therefore, we targeted birds that were already ringed (BTO rings) to increase the chance of recapture in the subsequent breeding season. The devices were recovered the following year (time on birds: median 360 days, range 351- 636 days) and on recovery there were no indications of injury or skin abrasion. There was no evidence from observations of breeding success, body mass or behaviour for a detrimental effect of the devices on the birds.

Data and analysis

Geolocator light-level data were downloaded from the devices with Integeo software (Migrate Technology Ltd). The data were analysed with R version 3.3.1 (R Core Team, 2016) using the package *FLightR* (Rakhimberdiev *et al.* 2015, Rakhimberdiev *et al.* 2017) to estimate position and stationary periods of > 3 consecutive twilights. Calibration location was the Farne Islands. The R package *BAStags* was used to examine twilight thresholds individually and correct for artefacts, particularly where the light detector was obscured from light by incubation behaviour. Data were corrected for clock drift for those devices that were still working on recovery (18 from the 2015 cohort and all 24 from the 2017 cohort). One of the devices fitted in 2015 that had stopped working before return had suffered a corruption (time/date shift) to time data for light levels due to water ingress; however, from the light-level data and known start position, the time frame was recreated by calibration to the local summer solstice and geographical origin. Data mapping and analysis were undertaken using *Maptools, Maps* and associated packages in R using the WGS84 coordinate reference system. Loxodromic bearings between points were calculated using the package *geosphere*. Comparisons between cohorts were undertaken using parametric (linear models) or non-parametric (asymptotic Wilcoxon-Mann-Whitney test [*Wilcox_test* function from the *coin* package for R] or standard Wilcoxon-Mann-Whitney signed rank test [base R, *Wilcox.test*]) procedures.

Data for Arctic Tern sightings in Great Britain and Ireland were obtained from the BTO *BirdTrack* database, described by Newson *et al.* 2016. These data comprised all sightings of Arctic Terns in the database up to 30 October 2017 by 1 km Ordnance Survey square; for analysis, these were converted to longitude and latitude coordinates for the centre of each 1 km square using the R packages *rnrfa*, *sp*, *rgeos*, and *rgdal*. Sightings within 20 km of the coast for the UK and island of Ireland were excluded and the remainder designated as ‘inland records’. These data were used ‘as is’ and we recognise that, given the difficulty of separating Common and Arctic Terns in the field, an unknown proportion of records may be incorrect.

RESULTS

Geolocator recovery

This analysis is based on data from 47 birds from both the 2015 and 2017 cohorts, which represent 47 outward and 43 inward movements in relation to the breeding area (Table 1). From observation or logger recovery, the mean overwinter return rate of geolocator-tagged birds was 92.5% (Table 1). In 2015, 29 control birds were fitted with a plastic leg ring (no geolocator), in addition to a conventional metal BTO ring on the other leg, and 24 (83%) of these were seen in subsequent years. These return rates are comparable to previous estimates of 82-87% for the annual survival or return rates of Arctic Terns at this colony (Coulson & Horobin 1976, Cullen 1957). Ten of the birds tagged in 2017 had previously been tagged in 2015 and have also been analysed separately where relevant.

Departure from the breeding area

After breeding, Arctic Terns are not constrained to remain near the colony until *Zugunruhe* initiates autumn migration, and may spend time in North Sea locations other than the Farne Islands before departure. *FLightR* can define relatively ‘stationary’ periods from sequential geolocator positions and, therefore, the date of departure from the last stationary period in the North Sea was taken to be the date of departure for autumn migration and the mean coordinates for these stationary periods defined as the departure points. Across the year cohorts, departure dates for 46 of the 47 birds were in the 25-day period from 17 July to 10 August; one bird in 2017 did not depart from the North Sea until 22 August (Table 2; Fig. 1). Although there was marginal evidence for a later departure in 2017 for the data as a whole (asymptotic Wilcoxon test, $0.1 > P > 0.05$, with or without the late-departing bird in 2017; Table 2), there was no indication from the 10 individuals tagged in both years for a significantly later departure in 2017 (one-sample Wilcoxon signed rank test on the individual differences between years, $P = 0.4$). Eight nests with tagged birds were known to have failed, three in 2015 and five in 2017; there was no significant difference in departure date for the tagged birds from ‘successful’ (chicks raised to fledging age or not known to have failed) and unsuccessful nests (asymptotic Wilcoxon test, stratified by year, $Z = -1.318$, $P = 0.19$).

Mean latitudes of the North Sea departure points ranged from 55.93° (approximately 80 km north of the Farne Islands) to 55.45° (approximately 140 km south of the Farne Islands) in 2015, and 56.82° (approximately 130 km north of the Farne Islands) to 55.52° in 2017 (Fig. 2). The departure latitudes had a more-northerly distribution overall in 2017 (asymptotic Wilcoxon test, $Z = -3.4303$, $P < 0.001$); however, for the 10 repeat birds there was no significant difference (one-sample Wilcoxon test, $P = 0.42$) suggesting that the more-northerly distribution of departure points in 2017 might be a characteristic of the sample of birds tagged rather than a result of environmental differences between years.

The median loxodromic bearings to the first geolocation position after departure were orientated approximately WSW of departure in both year cohorts (Table 2). The absence of North Sea geolocation points further south than the most southerly departure latitude (55.45°) and the distribution of geolocator-derived positions in the Irish Sea (Fig. 2), suggest that most birds flew over northern England to the Irish Sea before moving into the North Atlantic. Geolocator positions were more concentrated in the Irish Sea from the Cumbrian/Lancashire coast to the southern-most tip of Wales in 2017 compared to 2015 (Fig. 2B). In 2017, the geolocation positions for one bird suggest movement north along the North Sea coast, then west across the north coast of Scotland (Fig. 2B) into the North Atlantic, avoiding the Irish Sea entirely. Geolocator positions over Ireland for departing birds (five in 2015 and one in 2017; Fig. 2A,B) were consistent with the locations of various inland water bodies.

Arrival at the Farne Islands

Arrival of the birds back to the Farne Islands in 2016 and 2018 spanned a 26-day period, between 28 April and 22 May with no significant difference between years (Table 2). In contrast to the distribution of departure dates, the distribution of arrival dates tended to be skewed with most birds arriving in the period 30 April - 10 May (Fig. 1). The first-egg dates for Arctic Terns on Inner Farne were 14 and 17 May in 2016 and 2018, respectively. The directions of arrival, the loxodromic bearings from the Farnes to the last geolocator position before arrival, varied from 182° to 248° with no significant difference between years ($P > 0.5$; Table 2). However, arrivals were from a more-southerly direction (median 211.2°) than the bearings of departure (median 223.4°) for the sample of birds overall (both years combined, asymptotic Wilcoxon test, $Z = -4.447$, $P < 0.0001$), for individual birds (mean in-out difference of individual birds: -27.9°; one-sample Wilcoxon signed rank test for a mean of 0; $P < 0.0001$), and for the subset of repeat birds (differences: -21.5° , $P = 0.055$, and -27.9°, $P = 0.04$, for the 2015 and 2017 cohorts, respectively).

Other evidence for overland migration

To gain additional insight into possible overland migration, BTO *BirdTrack* records for Arctic Terns were analysed. Of 9054 inland records from 1966 to 2017, 99% were for the period 2001 to 2017. The majority of records were of birds in mid- to southern-England, with a tight spring peak in late April to early May (peak on 25 April), and a less-well defined increase of birds in the autumn (Fig. 3 inset). Broad patterns in the data suggest concentrations of sightings along three southwest to northeast lowland orientations (Fig. 3). The distribution and density of Arctic Tern sightings also broadly mirror the human population density of the UK (Anonymous 2017) and thus is likely to reflect birdwatcher density as well as the distribution of suitable stopover sites (water bodies) in lowland areas along potential Arctic Tern migration routes.

There is a noticeable cluster of *BirdTrack* records in southeast Wales (Fig. 3) similar to geolocator points for several incoming birds in 2016. Of 36 *BirdTrack* data points within longitudes -3° to -3.5° and latitudes 51.5° to 52.75°, 25 were from Llangorse Lake in the Brecon Beacons National Park, a shallow, low-lying lake of 153 ha and the second-largest fresh-water lake in Wales (Mullard 2014); 18 of the Llangorse Lake records were in April or May. From geolocator data for returning Farne Islands birds in 2016 (Fig. 2C), there were 17 geolocation points, relating to five birds, within the same area of southeast Wales and 11 of these within 11-30 km of Llangorse Lake. However, there were no geolocator positions in this area for returning birds of the 2017 cohort.

DISCUSSION

The absence of geolocator positions in the North Sea south of 54° latitude after departure from the Farne Islands, and the predominantly west and southwest geolocator positions for both years of the study, strongly suggest that, with one exception, these Arctic Terns crossed over the UK between the Irish Sea and the Farne Islands on migration. Geolocation points over Ireland, mainly in 2015, also suggest that some birds may enter the North Atlantic by crossing Ireland from east to west rather than through the Irish Sea. These results also suggest that this is a consistent migration strategy and not a result of particular weather conditions. However, within such an overall strategy, there may be variations in the distributions of geolocator positions between years that may relate to environmental factors. For example, the marked concentrations of geolocation positions in the Irish Sea in autumn 2017 suggest that birds may have been feeding there in preparation for migration. In contrast, there were fewer geolocation points in the same region in autumn 2015, suggesting that there are annual variations in foraging conditions, either before departure from the North Sea or at early stages in their subsequent migration. Good feeding conditions in the Irish Sea may also be a factor encouraging migration via an overland route across the UK rather than south into the Atlantic via the English Channel.

For incoming birds, many of the geolocation positions were in the Irish Sea with none in the North Sea south of the Farne Islands, suggesting that birds flew to the west coast of the UK and crossed to the Farne Islands overland, rather than entering the North Sea through the English Channel. This is consistent with observations of birds accumulating off the Lancashire coast in spring (White *et al.* 2012), and inferences that birds migrate overland after gaining height in the evening (Smith 2015). If migration across the UK is the rule rather than an exception, birds may not necessarily take the shortest route overland, as is suggested by trends in inland sightings and the more southerly directions of arrival compared to departure bearings. This idea is supported by the occurrence of geolocation points for five birds within an area of east Wales that has relatively frequent records of Arctic Terns in spring. Although there were no geolocation points in this area for birds returning in 2018, the presence of Arctic Terns at inland water bodies, both for departing and incoming birds, may relate to particular weather conditions (Kramer 1995) and represent convenient stopover locations for birds following a regular migration route. It is also interesting that the geolocator positions for Farnes birds had a more north-westerly bias than the inland

BirdTrack records, raising the question whether the *BirdTrack* records across south and east England relate to birds from Scandinavian and Baltic populations.

The results from this study also closely define the times of arrival of Arctic Terns at the Farne Islands and their departure from the North Sea. The timing of arrival (median 4-6 May) was broadly consistent with the slightly earlier peak (25 April) of inland UK visual records in spring and some 6 days earlier than at Troms, 1900 km further away in northern Norway (Barrett 2016). For Inner Farne between 1999 and 2018, the date of first egg has ranged from 12 - 19 May (mean 15 May; David Steel, pers. comm.), and was two days later in 2018 compared to 2016 (taking account of the leap year). This delay in breeding is consistent with a slightly later first-arrival date in 2018, and suggests that birds need around 15 days or so after arrival to attain breeding condition and establish pair bonds. The pre-breeding delay indicates that the Arctic Tern is an 'income' breeder and is dependent on local resources to achieve breeding condition (Bond & Diamond 2010). Monitoring for annual trends in timing of arrival and initiation of breeding may be important for assessment of long-term changes in local foraging resources. The range of departure dates from the North Sea was, apart from one bird in 2018, only a few days longer than for arrival, and similar between years. With the caveat that sample size was small and that breeding success or failure for a semi-precocial species in a dense colony can be hard to determine with confidence, there was no evidence of a relationship between departure date and breeding success, suggesting that migration scheduling is tightly regulated relative to seasonal progression.

The *FLightR* software used for data analysis has a reported accuracy of around 50 km (Rakhimberdiev *et al.* 2016), and the times of arrival and departure were outside the spring and autumn equinox periods. Nevertheless, observations of birds gaining height prior to migration overland (Smith 2015) raise an issue with respect to the accuracy of geolocation data in general because geolocators on birds at height will record delayed twilights compared to the same devices at sea level, producing errors in geolocation. However, there is circumstantial evidence to increase confidence in the accuracy of geolocator positions. For example, overland geolocation points often occurred in areas with extensive water bodies, and which also have had relatively frequent sightings of Arctic Terns. Furthermore, the tight band of geolocation points in the Irish Sea from the Cumbrian/Lancashire coastline to the southernmost tip of Wales for many birds in autumn 2017, supports an accuracy of location to at least 50 km.

Overland migration may be more common for seabirds entering and leaving the North Sea from the North Atlantic than has been appreciated. For Arctic Terns, the drivers of an overland migration strategy are unknown, but may be the shortest and most energy-efficient route for rapidly arriving at the breeding colony in spring. Alternatively, the strategy may relate to the locations of good feeding resources, both at the start of autumn movement south through the North Atlantic (Fijn *et al.* 2013), and towards the end of northward migration in the spring. Furthermore, Arctic Terns have one of the longest migrations known, encompassing coastal, oceanic and polar regions at a global scale (Egevang *et al.* 2010, Fijn *et al.* 2013). Given the scale of annual migration from north to south polar regions, smaller-scale terrestrial environments may be insignificant constraints to direct migration. In a broader context, land may be less of a barrier to seabird migration than anticipated.

We would like to thank BBC Springwatch and Migrate Technology for generously funding the purchase of geolocators in 2015, and members of the Natural History Society of Northumbria who, together with a grant from the Seabird Group, funded geolocator purchase for the 2017 study. We would also like to thank the BTO for the BirdTrack data for Arctic Terns, and the National Trust, the Farne Islands Ranger Team and David Steel for their support and encouragement of the study. We also thank the Natural History Society of Northumbria for their additional support, encouragement and interest in the project, and the reviewers and associate Editor, Lauren Pichegru, for comments which improved the manuscript.

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Table 1: Summary of geolocator recovery; all geolocators yielded data, but incomplete trips were recorded for 5 geolocators from the 2015 cohort, although one of these stopped working only after arrival at the breeding colony.

	2015 cohort	2017 cohort	Summary
Geolocators fitted	28*	25	53
Geolocators recovered	23**	24	47
Outward migration data (birds)	23***	24	47
Inward migration data (birds)	19	24	43
Overwinter return/survival for year 1	89%**	96%	92.5% (Mean)

**Of 28 birds tagged initially, one was found dead, cause unknown (and with no obvious external injury), in the colony during the season but without its geolocator or mounting ring and this bird is discounted from the overwinter return/survival rate.*

*** 21 recovered in 2016 and two in 2017 and an additional bird from this cohort was seen in 2018 but not recaptured, giving an overall known overwinter return for year 1 of 24/27 birds.*

**** One geolocator recovered in 2017 yielded data for two outward (2015, 2016) and one inward (2016) trips. For consistency only the 2015 outward trip has been included.*

Table 2: Departure from the North Sea and spring arrival at the Farne Islands

	2015 cohort	2017 cohort	Year comparisons
Departure			
Date range	17 July – 10 August 2015	17 July – 22 August 2017	
Median date	25 July 2015	4 August 2017	*P* = 0.06[¶]
Bearing range	203.8 - 268.7°	171.1 - 337.1°	
Median bearing	222°	224°	*P* = 0.47[‡]
Latitude range	54.45 - 55.93°	55.52 - 56.82°	
Arrival			
Date range	28 April – 22 May 2016	2 May – 20 May 2018	
Median date	4 May 2016	6 May 2016	*P* = 0.46[#]
Bearing range	181.9 - 236.5°	190.6 - 248.1°	
Mean bearing	208.3°	213°	*P* = 0.54[#]

[¶]Asymptotic Wilcoxon-Mann-Whitney Test, all data *P* = 0.062; data excluding one late-departing bird in 2017, *P* = 0.094.

[‡]Asymptotic Wilcoxon-Mann-Whitney test, unstratified or stratified by repeat status.

[#]Asymptotic Wilcoxon-Mann-Whitney test

FIGURE LEGENDS

Figure 1. The distributions of dates (day in year) of departure (top panel) and arrival (bottom panel) of geolocator-tagged Arctic Terns on the Farne Islands grouped by 5-day periods for the two cohorts combined. The hatched proportion of each bar refers to the 2015 cohort and the dark-grey shading to birds from the 2017 cohort. Dates at the start and end of the horizontal axis are shown; 2016 was a leap year.

Figure 2. Geolocation points for the departure (A, 2015; B, 2017) and arrival (C, 2016; D, 2018) of Farne Islands Arctic Terns. The location of the Farne Islands is marked by a large triangle. The main sea areas are labelled on A. Different symbols are used for each bird, with the same symbols (per bird) used for departure and arrival geolocation points in A&C and in B&D. In A and B, the location of the mean stationary points immediately before departure for each bird are indicated by filled black circles with errors bars indicating the standard deviations of latitude and longitude. Thin lines are used to join geolocation points for each bird only to indicate temporal relationships and these are not intended to represent movement trajectories.

Figure 3. The locations of inland (> 20 km from the coast) sightings of Arctic Terns in the BTO BirdTrack database. Record locations (filled circles) are overlaid onto a 20 x 20 km square gridded record-density plot, where grey intensity (vertical scale bar to the right) represents the number of records (some records may involve several birds). The black arrow indicates the area of Llangorse Lake in south Wales; lettered grey arrows indicate sighting locations oriented along three south-west to north-east lowland areas corresponding to the Trent River and floodplain (a), north of the North Wessex Downs and Chiltern escarpment (b) and the Thames floodplain (c). The number of records per day for the ~9000 records is shown as an inset graph in the top left, with day as day in the year on the horizontal axis. For orientation: day 100 (in a normal year) is 10 April, and day 150 is 30 May.

Figure 1

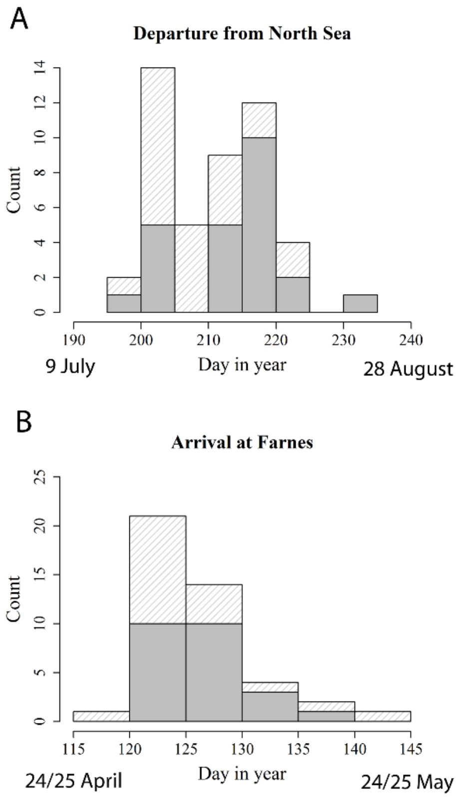

A
Departure from North Sea
Count
0
2
4
6
8
10
12
14
190
200
210
220
230
240
Day in year
9 July
28 August
B
Arrival at Farnes
Count
0
5
10
15
20
25
115
120
125
130
135
140
145
Day in year
24/25 April
24/25 May

Figure 2

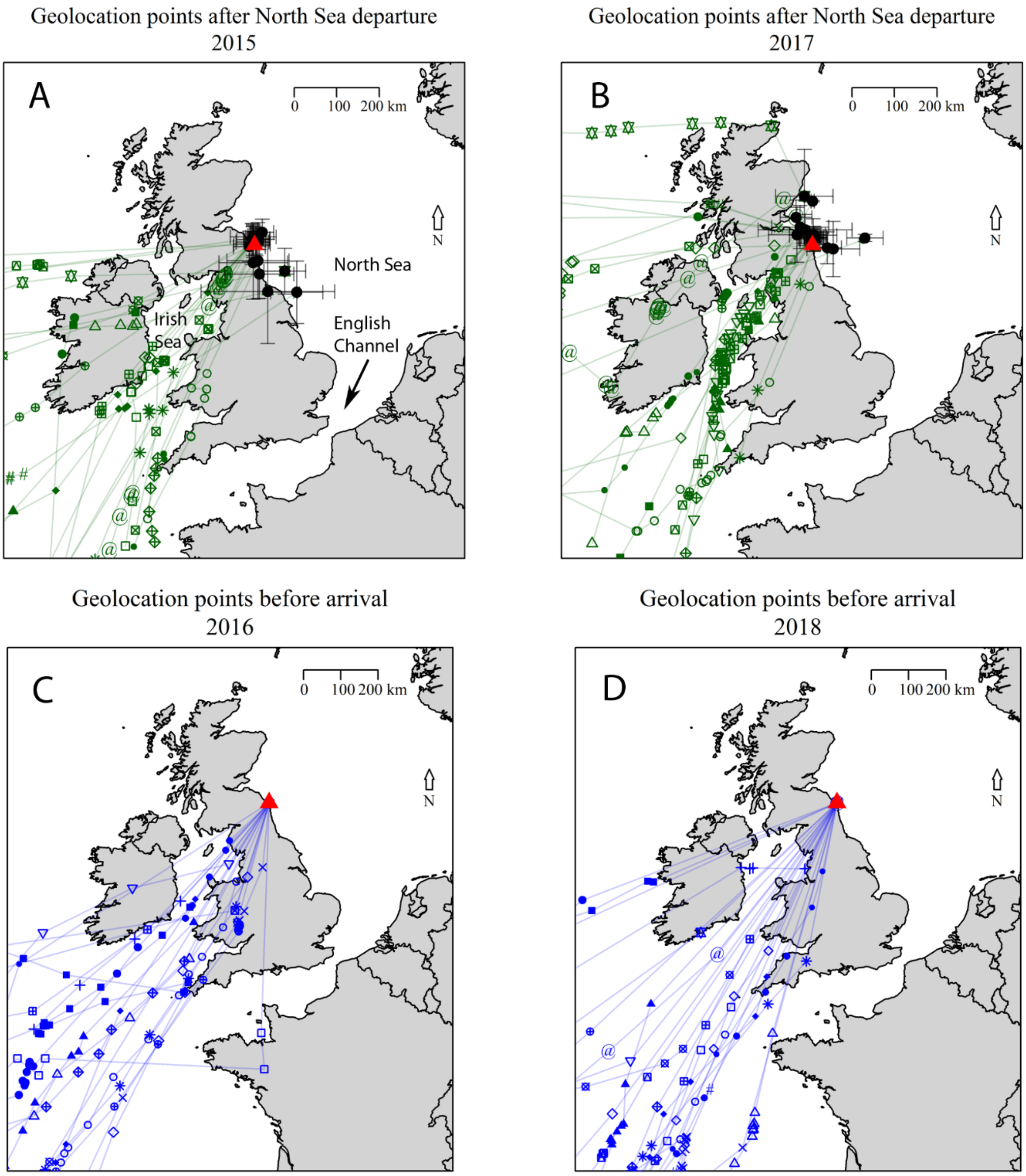
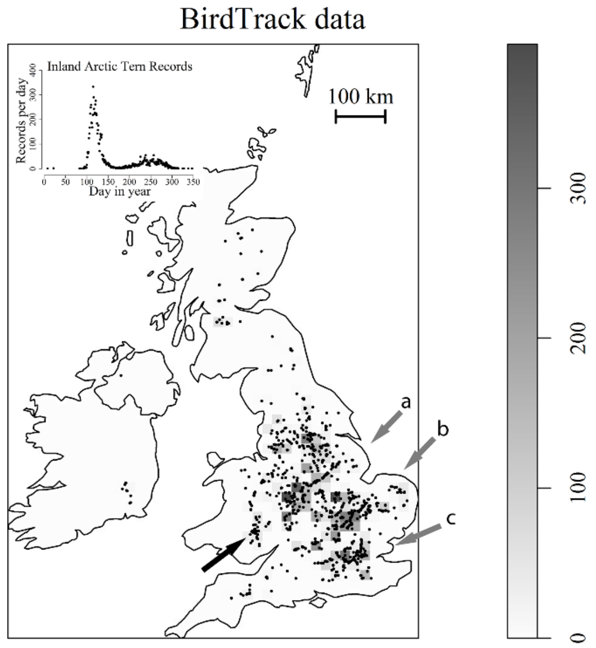

Geolocation points after North Sea departure
2015
A
0 100 200 km
N
North Sea
Irish
Sea
English
Channel
Geolocation points after North Sea departure
2017
B
0 100 200 km
N
Geolocation points before arrival
2016
C
0 100 200 km
N
Geolocation points before arrival
2018
D
0 100 200 km
N

Figure 3


BirdTrack data
Inland Arctic Tern Records
Records per day
0
100
200
300
400
0
50
100
150
200
250
300
350
Day in year
100 km
a
b
c
0
100
200
300